

Phylogenetic and Taxonomic Studies on *Helonias*, *Ypsilandra* and *Heloniopsis*

II. Evolution and Geographical Distribution

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This paper focuses on the following three evolutionary facets of the *Helonias* group (incl. *Helonias*, *Ypsilandra* and *Heloniopsis*): (1) process of the phylogenetic differentiation, (2) trends in the floral evolution, and (3) historical aspect of the geographical distribution. As regards (1), a phylogram of this plant group is presented based chiefly on the morphological data. Both *Helonias* and *Ypsilandra* are paraphyletic, while *Heloniopsis* is monophyletic. *Heloniopsis* is divided tentatively into two subgroups, HP-1 and HP-2. In this paper HP-1 is suggested to paraphyletic, while HP-2 monophyletic. The phylogenetic evolution is presumed to have proceeded in the following sequence; *Helonias* → *Ypsilandra* → HP-1 → HP-2. Concerning (2), there exists a trend toward the development of some specific structures that appear to be suited for pollination by insects foraging for nectar. There is also another remarkable trend toward the development of the elongate style. As for (3), the most primitive genus, *Helonias*, is distributed in North America, while the two descendant genera (*Ypsilandra* and *Heloniopsis*) are distributed in Asia. Considering the evolutionary sequence shown above, it seems likely that in Asia the range of the *Helonias* group has extended from west to east and then to northeast, as the phylogenetic evolution proceeded.

In the preceding papers (Tanaka 1997c, 1997d), the results of comparisons of various characters of the three genera have been reported with some brief remarks on the phylogenetic relationships among the species. In this paper, further remarks will be made regarding the three evolutionary facets of this plant group based chiefly on my own observations (Tanaka 1997a–d).

As in my previous papers (Tanaka 1997c, 1997d), the name of each species of the three genera is abbreviated here as follows: *Helonias bullata* L. = **Bu**, *Ypsilandra yunnanensis* W.W. Smith & J.F. Jeffrey = **Y**, *Y. alpina* Wang & Tang = **A**, *Y. cavaleriei* Lévl. & Vaniot = **C**, *Y.*

thibetica Franch. = **T**, *Heloniopsis leucantha* (Koidz.) Honda = **L**, *H. umbellata* Baker = **U**, *H. kawanoi* (Koidz.) Honda = **K**, *H. orientalis* (Thunb.) C. Tanaka = **O**, and *H. breviscapa* Maxim. = **Br**.

As **C** could not qualitatively be distinguished from **T** in any characters (Tanaka 1997c–d), **C** is tentatively treated here as being included in **T**. Consequently, this paper deals with nine species in total. For the taxonomic circumscription of **Br**, see Tanaka (1997b).

In this paper, *Heloniopsis* is tentatively divided into two subgroups; **HP-1** and **HP-2**. The former includes **L**, **U** and **K**, while the latter includes **O** and **Br**. The latter subgroup

differs from the former in having the character states 7-a and 7-b listed in Table 1.

A group of plants belonging to the three genera is called here the “*Helonias* group”.

Materials on which this paper is based are the same as those described in my previous papers (Tanaka 1997a, 1997b). For determining the geographical ranges of the species, I examined many herbarium specimens (Tanaka 1997a, 1997b) as well as much literature (Miyabe and Kudo 1932, Chong 1957, Hara et al. 1978, Utech 1978, Chen 1980, Yang 1991, Noltie 1994, etc.).

(1) Process of the phylogenetic differentiation

According to my previous studies (Tanaka 1997a–d), in many characters the character state differs among the species. Among those, there are some characters whose evolutionary direction (or polarity) can be presumed without much difficulty. For example, in the characters of both the style and the nectary, there are different character states among the species respectively, and the evolutionary process of the development in these characters seems fairly traceable (Tanaka 1997c–d). Knowledge obtained from the observations on these characters was naturally made much of when I attempted to elucidate the process of the phylogenetic differentiation of the *Helonias* group. Fig. 1 shows the phylogram of this plant group constructed on the basis of the results of my own observations (Tanaka 1997a–d). The character states adopted for this construction of the phylogram are listed in Table 1. As this phylogram shows, the phylogenetic evolution is presumed to have proceeded from *Helonias* through *Ypsilandra* to *Heloniopsis*. Both *Helonias* and *Ypsilandra* are respectively regarded as paraphyletic, while *Heloniopsis* is monophyletic. *Heloniopsis* is tentatively divided here into two subgroups; HP-1 and HP-2, as mentioned earlier. In this case, HP-1 is

paraphyletic, while HP-2 monophyletic.

It is difficult to specify the sister group of the *Helonias* group, but one of the most likely candidates for it seems to be the *Chamaelirium-Chionographis* group. In this paper I tentatively adopted a character state, O-a (cf. Table 1), as an apomorphy characterizing a common ancestral lineage of both *Bu* and *Y* (Fig. 1). This adoption is based on the following two reasons: 1) This character state is formed by adnation between two different floral organs. This means that this character state is ‘secondary’ in terms of the organizational level compared with the state displaying no such adnation. 2) As far as I know, this character state is unique among the related genera (e.g., Melanthioideae-Helonieae (Krause 1930), to which both *Chamaelirium* and *Chionographis* belong). Needless to say, it is necessary to search further for the sister group of this plant group.

The phylogram shown in Fig. 1 is based chiefly on the morphological data. Further studies including molecular analyses are desirable in order to elucidate the evolutionary history of this plant group.

(2) Trends in the floral evolution

Below I briefly summarize some of the floral characters of the *Helonias* group and describe some evolutionary trends recognized there. Most of the data on which the following statements are based have been reported in the previous papers (Tanaka 1997a–d).

Fig. 2 shows the diagrams of the floral structure of seven species arranged in accordance with the presumed evolutionary sequence (cf. Fig. 1). In both *Helonias* (Fig. 2; *Bu*) and *Ypsilandra* (Fig. 2; *Y*, *A* and *T*), the base of the inner filament is adnate to the base of an ovary, while that of the outer filament is not. The base of each tepal in the two genera does not form any distinct nectary hollow. Anthers are extrorse in *Helonias*, but when fully dehiscent

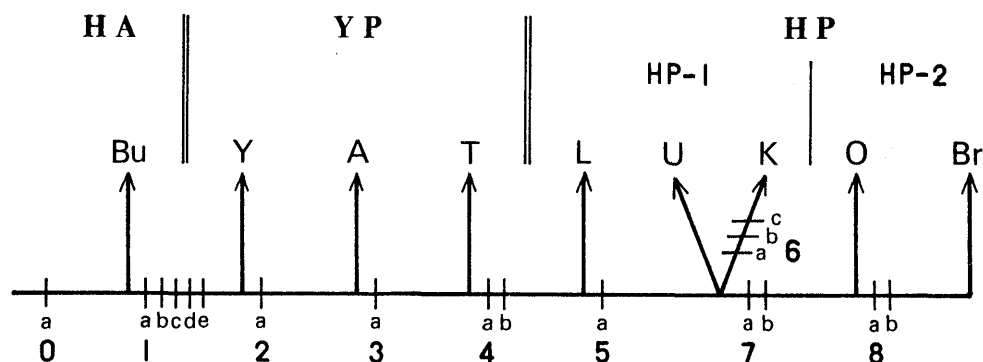


Fig. 1. A phylogram of the *Helonias* group. In the upper part is indicated a classificatory division. HA: *Helonias*, YP: *Ypsilandra*, HP: *Heloniopsis*. HP-1 and HP-2 are tentative subdivisions of HP (see the text). Codes such as 0-a, 1-a, 1-b, 6-a, ... represent character states. For information of these codes, see Table 1. Bu, Y, ... are abbreviations of the species names (see the text).

Table 1. Character states used for the construction of the phylogram of the *Helonias* group in Fig. 1. Character codes (below left) correspond to those in Fig. 1. For the code 0-a, see also the text.

Code	Character state
0-a	The base of the inner filament becomes adnate to the base of an ovary
1-a	Connation of three styles proceeds
1-b	Width of seeds becomes narrower
1-c	Number of seeds per loculus increases
1-d	Number of flowers per inflorescence decreases
1-e	Longitudinal groove between thecae is lost
2-a	Connation among three styles proceeds
3-a	Connation among three styles proceeds
4-a	Inner filaments become free from an ovary
4-b	Confluent part between thecae becomes narrower and degenerative
5-a	Racemes become more like umbels
6-a	Flowering season shifts (from spring) to summer to autumn
6-b	Inflorescences become bracteate
6-c	Overall size of a plant is reduced
7-a	A tepal and its corresponding filament become adnate to each other at their base
7-b	Neighbouring tepals become connate to each other at the base
8-a	Leaves become thinner
8-b	Nectaries become located in higher position

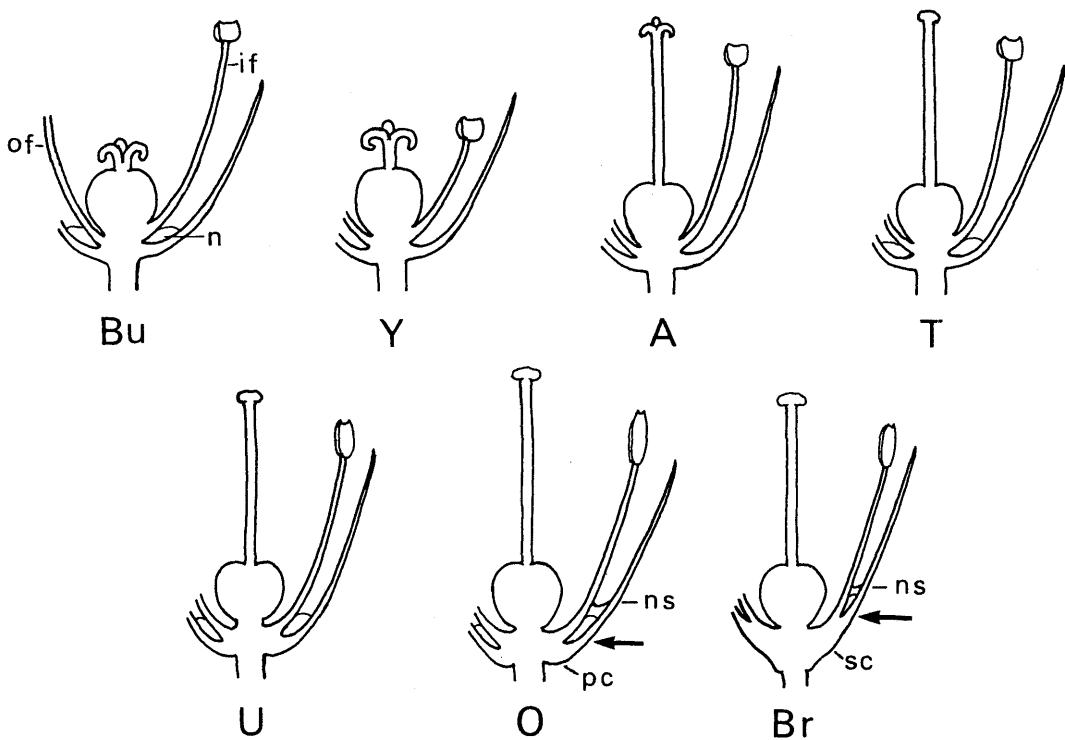


Fig. 2. Diagrams of the floral structure of seven species of the *Helonias* group, arranged in the presumed evolutionary sequence; $Bu \rightarrow Y \rightarrow A \rightarrow T \rightarrow U \rightarrow O \rightarrow Br$ (cf. Fig. 1). if: inner filament, of: outer filament, n: nectar, ns: saccate structure of a nectary formed by adnation between a filament and a tepal, pc: primary convex, sc: secondary convex. Arrows indicate the level of the bottom of a nectary sac. Anthers depicted are dehiscent ones. Secretion of nectar in *Y* and *A* has not been confirmed yet (cf. Tanaka 1997a, 1997c). The membranous structure formed by connation between neighbouring tepals in *O* and *Br* is not depicted. For "pc" and "sc", see Tanaka (1997b).

they look to be latrorse. Anthers of *Ypsilandra* are latrorse. Anthers of these two genera are unilocular and the confluent part between thecae are relatively broad. While, in *Heloniopsis* (Fig. 2; *U*, *O* and *Br*), both the inner and the outer filaments are free from an ovary. The base of each tepal in *L*, *U* and *K* forms more or less a nectary hollow. The same part of each tepal in *O* and *Br* is adnate to the base of the corresponding filament and forms a deeper nectary sac. In *Br*, the nectary is located higher in relative position compared with that in the other species, and some associated morphological changes occur intraspecifically in the basal part of the flower (Tanaka 1997b). Anthers are extrorse to subextrorse, but when

fully dehiscent they look to be latrorse. The confluent part between thecae is narrower in *Heloniopsis* than that in the two other genera, and more or less rudimentary.

There seems to be the following trend in the floral evolution of the *Helonias* group. In *Heloniopsis*, compared with the two other genera, the base of a filament is located closer to its corresponding tepal (Fig. 2). In *O* and *Br*, these two different floral organs become adnate to each other at their base and form a deep nectary sac, as stated above. Further, due to this approximation of the two floral organs, the space between the two organs necessarily becomes narrower. As a consequence, when insects come into this narrow space to suck

nectar at the bottom, they are likely to get smeared with pollen by the anthers located near the mouth of the space. The anthers of *Heloniopsis*, which are extrorse to subextrorse and narrow at their terminal end, appear to be suited for smearing their pollen on the insects coming into this narrow space. These observations suggest that the two floral organs of *Heloniopsis* tend to function as a set. This set apparently serves as an apparatus for ensuring pollination by insects foraging for nectar¹⁾. Each flower of *Heloniopsis*, particularly of *O* and *Br*, is regarded as comprising 6 such unitary apparatus. Contrarily, in the flowers of both *Helonias* and *Ypsilandra* there is no particular indication that the two floral organs tend to function as a set. From all these observations, it could be said that in the floral evolution of the *Helonias* group there is a trend toward the development of the apparatus (designated here as **SA**), and the development of this trend is strongly associated with insects visiting the flowers for nectar.

Further, in the flowers of both *O* and *Br*, a membraneous structure is developed between the neighbouring apparatus (tepals) at their base (Tanaka 1997b). It is obvious that this structure reinforces the base of the apparatus structurally by connecting them, and helps to prevent the flowers from suffering physical damages which might possibly be caused by the insects visiting the apparatus for nectar. Therefore, the development of this structure (designated here as **SB**) seems also to be strongly connected with those insects.

The relative position of the nectary in *Br* is higher than any other species, as mentioned above. The development of this characteristic (designated here as **SC**) must also be deeply associated with the insects visiting the apparatus for nectar (cf. Tanaka 1997b).

As far as we see the developments of these three floral characteristics (**SA**, **SB** and **SC**), the floral evolution in this plant group is said to

be progressive, and in this meaning, it might also be called anagenetic (cf. Lincoln et al. 1982, for the term anagenetic or anagenesis). The pollinator strongly associated with this anagenetic floral evolution is apparently the insects foraging for nectar, not for pollen, even if both forage types of insects may actually visit and pollinate the flowers (cf. Takahashi 1988, for pollinators in *O*).

Meanwhile, the styles of this plant group also show the presence of another remarkable evolutionary trend (Fig. 2). The columnar part of the style is presumed to have elongated in the course of evolution (Tanaka 1997c). This elongation seems to have helped the stigma to receive pollen more effectively from the insects. The development of the elongate style may not necessarily be connected only with the insects foraging for nectar.

It is obvious that in the course of evolution the flowers of the *Helonias* group have strengthened their ties with the insects foraging for nectar, as described above. But, at the same time, they also seem to have been keeping close contact with the insects foraging for 'pollen' as possible pollinators. In fact, it is observed by Takahashi (1988) that both forage types of insects actually visit and pollinate the flowers of *O*.

In the future it is desired to make observations of the pollinators in the various species of this plant group. There is no doubt that these observations greatly help our understanding of the floral evolution of this plant group.

(3) Historical aspect of the geographical distribution

The ranges of *Helonias* and two other genera (*Ypsilandra* and *Heloniopsis*) are widely separated geographically. While the former has its range in eastern North America (Fig. 3, above left), the latter two genera have their ranges in eastern Asia (Fig. 3). Currently, it is difficult to trace thoroughly the historical proc-

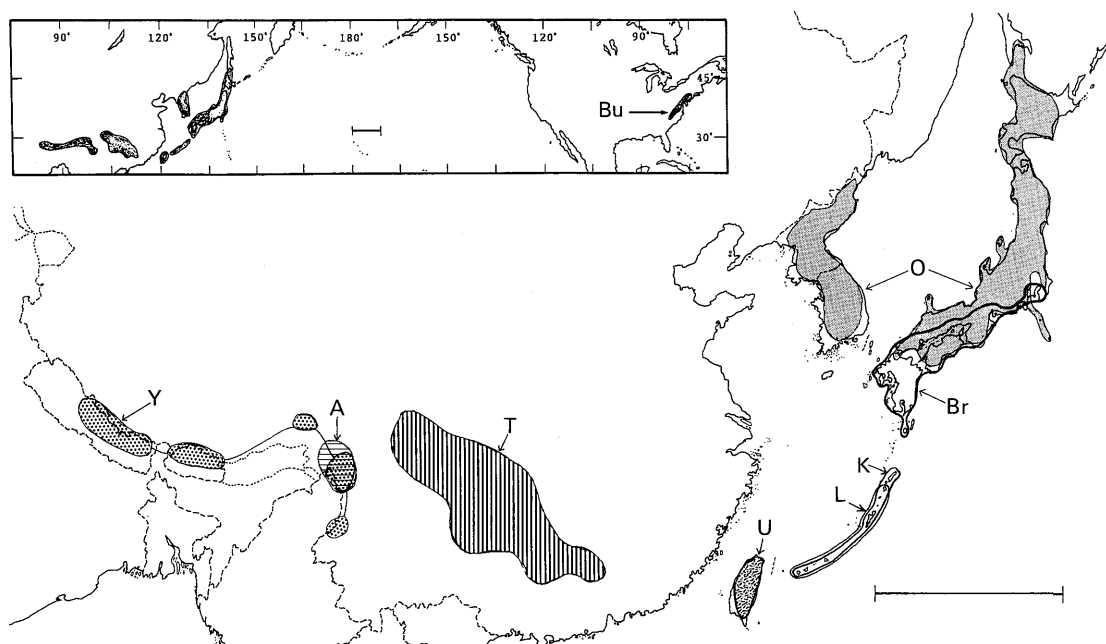


Fig. 3. Approximate geographical ranges of nine species of the *Helonias* group. Scale bars indicate 1,000 km. A monotypic genus, *Helonias* (*Bu*), is distributed in North America (see the above left map), while *Ypsilandra* (*Y*, *A* & *T*) and *Heloniopsis* (HP-1: *L*, *U* & *K*. HP-2: *O* & *Br*) are in Asia. In Asia, the range of this plant group is presumed to have extended from west to east and then to northeast, as the phylogenetic evolution proceeded (*Ypsilandra* → HP-1 → HP-2; see also the text and Fig. 1).

ess of the establishment of this disjunctive distribution. But, one possible explanation for this disjunctive distribution seems to be as follows. According to Tanai (1988), the temperate deciduous broad-leaved forest (the so-called Arcto-Tertiary flora) was distributed around the Arctic region in mid and late Eocene. In response to a cooling climate since the end of Eocene, the forest began to extend southward (Tanai 1988). It seems likely that the *Helonias* group also followed the same history as this forest. That is, the group once distributed somewhere in the periphery of the Arctic region is presumed to have migrated southward, with the migration of the forest. This southward migration seems to have been the major cause for such a large scale disjunctive distribution of this plant group. *Bu* distributed in N. America is regarded as the most primitive species (among the nine species of the

Helonias group), while all the other species in Asia are regarded as its descendants (cf. Fig. 1). Therefore, there seems to be a possibility that the southward migration of this plant group occurred in the very early stage of its phylogenetic differentiation.

In Asia, *Ypsilandra* (*Y*, *A* and *T*) has its range west of that of *Heloniopsis* (*L*, *U*, *K*, *O* and *Br*) (Fig. 3). One of the two subgroups of *Heloniopsis*, HP-1 (*L*, *U* and *K*), has its range southwest of the range of another subgroup, HP-2 (*O* and *Br*). Between the range of *Ypsilandra* and that of HP-1 there is the Taiwan Strait, and between the range of HP-1 and that of HP-2 the Tokara Strait. Most of the areas covered by *Heloniopsis* are insular.

Meanwhile, these three groups of plants are presumed to have evolved in the following sequence; *Ypsilandra* → HP-1 → HP-2 (Fig. 1). If this presumption is correct, it seems

likely that the range of the *Helonias* group in Asia has extended from west to east and then to northeast, as the phylogenetic evolution proceeded. However, within each range of the three groups (*Ypsilandra*, HP-1, HP-2), especially within that of HP-1 and HP-2, some irregularity is present concerning the direction of the range extension.

Endnote

¹⁾In this paper “the insects foraging for nectar” does not mean to include all these kinds of insects. For instance, the insects which suck nectar but do not or scarcely participate in the pollination of this plant group are not meant. The kinds and the behaviour of the insects visiting the flowers of *O* are reported by Takahashi (1988).

References

- Chen S-C. 1980. *Ypsilandra*, pp. 15–18. In: Wang F.-T. and Tang T. (ed.), *Flora Reipublicae Popularis Sinicae*, Tomus 14. Science Press, Beijing.
- Chong, T-H. 1957. *Heloniopsis*, p. 961. Korean Flora. 2 (Herbaceous plants). Synji Sa, Seoul.
- Hara H, Stern W. T. and Williams L. H. J. 1978. *Ypsilandra*, p. 80. An Enumeration of the Flowering Plants of Nepal. Vol. 1. British Museum, London.
- Krause K. 1930. Melanthioideae-Heloniaceae, pp. 257–260. In: Engler A. und Prantl K. (ed.), *Die Natürlichen Pflanzenfamilien*. 15a. Wilhelm Engelmann, Leipzig.
- Lincoln R. J., Boxshall G. A. and Clark P. F. 1982. A Dictionary of Ecology, Evolution and Systematics. Cambridge University Press, Cambridge.
- Miyabe K. and Kudo Y. 1932. *Heloniopsis*, pp. 309–310. Flora of Hokkaido and Saghalien. III. Monocotyledoneae. Araceae to Orchidaceae. Journ. Fac. Agr. Hokkaido Imp. Univ. 26(3).
- Noltie H. J. 1994. *Ypsilandra*, pp. 90. Flora of Bhutan. 3(1) Royal Botanic Garden Edinburgh, Edinburgh.
- Takahashi H. 1988. The pollination biology of *Heloniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae). Pl. Sp. Biol. 3: 117–123.
- Tanai T. 1988. Kaede-zoku no shinnka (Evolution of the genus Acer), pp. 106–112. In: Kawano S. (ed.) Newton. Special issue. Shokubutsu no sekai. No. 3. Kyoikusha, Tokyo (in Japanese).
- Tanaka N. 1997a. Taxonomic significance of some floral characters in *Helonias* and *Ypsilandra*. J. Jpn. Bot. 72: 110–116.
- 1997b. Evolutionary significance of the variation of the floral structure of *Heloniopsis*. J. Jpn. Bot. 72: 131–138.
- 1997c. Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis*. I. Comparison of character states (1). J. Jpn. Bot., 72: 221–228.
- 1997d. Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis*. I. Comparison of character state (2). J. Jpn. Bot., 72: 286–292.
- Utech F. H. 1978. Vascular floral anatomy of *Helonias bullata* (Liliaceae-Heloniaceae), with a comparison to the Asian *Heloniopsis orientalis*. Ann. Carnegie Mus. 47: 169–191.
- Yang G.-H. 1991. *Ypsilandra*, pp. 11–13. Flora Sichuanica. 7. Sichuan Folk Press, Chengdu.

田中教之：*Helonias*, *Ypsilandra*, *Heloniopsis* の系統と分類 II. 進化と地理的分布

これまでの観察結果 (Tanaka 1997a–d) に基づいて、表題の3属 (本文では *Helonias* group と呼んだ) の進化に関する次の三つのテーマ、すなわち (1) 系統分化の過程、(2) 花部構造に見られる進化傾向、および (3) 地理的分布の歴史的側面、について述べた。本稿では *Heloniopsis* (ショウジョウバカマ属) を2亜群、HP-1 と HP-2、に分けた。この2亜群への分類は仮処置である。HP-2 は形質 7-a と 7-b (表1) を持つことで HP-1 から区別できる。HP-1 は L, U, K の3種を含み、HP-2 は O と Br の2種を含む (種名の略号については本文を参照されたい)。

(1) に関して：主として形態的特徴に基づいて作成した系統分岐図を図1に示した。本植物群は *Helonias* → *Ypsilandra* → *Heloniopsis* (HP-1 → HP-2) の順に進化したと推定した。この系統樹では、*Helonias* は側系統、*Ypsilandra* は側系統群、

Heloniopsis は単系統群と見なされる。*Heloniopsis* を HP-1 と HP-2 の2亜群に区別した場合には、HP-1 が側系統群であり HP-2 は単系統群である。

(2) に関して：*Helonias* と *Ypsilandra* では内花糸の基部が子房と合生しているが、*Heloniopsis* では内花糸の基部が子房から離生し (図2)、花糸の基部とそれに対生する花被片との間隔が他の2属のそれよりも相対的に狭まる傾向がある。とくに O と Br では、この2花部器官 (1雄ずいとそれに対生する1花被片) が基部で合生し鞘状の蜜槽を形成するようになる。また、これらの2花部器官が近接することで、これら2器官の間の蜜槽に通じる空間が狭まる傾向が生じる。葯はこの空間の入口付近に位置しているので、蜜槽の蜜を得るために2花部器官の狭い空間に進入しようとする昆虫の体に、花粉が付きやすくなると考えられる。*Ypsilandra* の葯が側向的 (latrorse) で、上部の半

葯間の連合部分が巾広いのに対して、*Heloniopsis* の葯は外向的 (extrorse) ないしは準外向的 (subextrorse) で、葯の頂部は相対的により狭くなっている。後者 (*Heloniopsis*) の葯の形態は、この空間に出入りする昆虫の体に花粉を付着させるのにより適していると思われる。このような観察から、*Heloniopsis* の2花部器官は1セットとして機能する傾向、すなわち、協同して、受粉を成功に導く一種の装置 (SAとする) として機能する傾向を持っていると考えられる。さらにOとBrでは、この装置の基部間に膜状の構造 (SBとする) が発達している。この構造は隣接する装置の基部どうしを連結することによって、装置を構造的に強固にすることに貢献していると思われる。この構造の発達もまた、蜜を得るために装置を訪れる昆虫と深い関わりを持っていると考えられる。Brの花では蜜槽が他の種のそれよりも相対的に高い位置にある (SCとする) 傾向が見られるが、この性質の発達もまた、吸蜜のためにその装置を訪れる昆虫と深く関わっていると推定される。以上述べたような特別な花部構造 (SA, SB, SC) の発達は、蜜を求めて花を訪れる昆虫と深い関わりを持つものであり、花粉を求めて花を訪れる昆虫ととくに関わるものではない。

一方、本植物群の花柱 (3花柱が合生して単一

の柱状構造をとっている部分) は伸長する方向で進化したと推定されるが、この進化傾向は、蜜を得ようとして訪花する昆虫だけに必ずしも関わるものではないと考えられる。Takahashi (1988) が報告しているように、Oの花には蜜を得ようとする昆虫も花粉を得ようとする昆虫も訪れる。

(3) に関して：本植物群を四つの群 (*Helonias*, *Ypsilandra*, HP-1, HP-2) に分けて扱った場合、相対的にもっとも原始的と考えられる *Helonias* は北米東部に、次に原始的と考えられる *Ypsilandra* はヒマラヤから中国にかけて分布し、その次に原始的な HP-1 は台湾と琉球に分布し、もっとも進化した群と推定される HP-2 は鹿児島県以北の日本、韓国、北朝鮮、そしてサハリン南部に分布している。北米とアジアに本植物群が大きく隔離分布しているが、これはかつて周北極地域に分布していたと推定される本群が気候の寒冷化とともに南下したことがその隔離分布の主な原因となっているように思われる。アジア地域においては、本群の分布域は、系統進化とともに、西から東へ、さらに東北方向へ拡大した可能性がある。ただし、各群の内部、とくに HP-1 と HP-2 の各内部では、進化に伴う分布域の拡大の方向は必ずしも一定しない (図3)。

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